STUDIES IN THE LIFE-HISTORIES OF AUSTRALIAN ODONATA.

No. 4. Further notes on the life-history of Petalura gigantea Leach.

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(Plate vii.)

Since the publication, in 1909*, of my paper on the life-history of *Petalura gigantea* Leach, I have collected a considerable amount of new and interesting information about it. This is now included in the present paper, and brings the study of this remarkable species much closer to completion.

After I had obtained the supply of exuviæ from the Leura swamp (Blue Mountains), in 1908, I determined, if possible, to find the living larva. For this purpose, I visited Leura in October, 1909, and searched the swamp carefully, collecting mud from various "pot-holes" and examining it, and also dredging the larger holes in the swamp. No success attended these efforts. However, during a visit to Medlow, Blue Mountains, in the middle of November, 1909, I found a fairly large and conveniently situated swamp, over a restricted portion of which the *Petalura* exuviæ were found clinging to the reed-stems. The next morning I got up about 5.30 a.m., and visited this swamp. As I expected, the *Petalura* larvæ were emerging in fair numbers, and many were only just climbing out of the swamp. As I particularly wanted to examine the gizzard of the larva, I collected half-a-dozen quickly into a box, and returned with them. But so rapidly was the final change approaching,

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that, by the time I got back, they were all emerging in the box. In any case, the actual internal metamorphoses had proceeded too far for an examination of larval structures, even if I had attempted it the moment I took them.

Returning to the swamp, I set about trying to solve the problem, where and how the larvæ lived. My friend, Dr. F. Ris, to whom I had sent specimens of the exuviæ, had pointed out to me that, in every case, the anal opening was wide open in the cast-skin. This fact led him to believe that these larvæ were not aquatic, but air-breathers. Bearing this in mind, I selected a large clump of sedge in the middle of the swamp, to which three exuviæ were clinging, and carefully examined the clump itself. Close to the base of the stalk on which the first exuviæ were found, I discovered a neat round hole, about half-an-inch in diameter. On examining the bases of the other two stalks which carried exuviæ, I found similar holes. Passing on to other clumps, I found that, in every case where there were exuviæ on the reed-stems, a neat, round hole occurred close by, near the base. Next, with a knife, I cut away the edge of one of the holes, and followed it down. It was very damp, and the sides smooth and plastered with the soft mud of the swamp, enclosing the matted roots of the sedge. At the water-level the hole was, of course, full of water, and thence downwards it got looser, finally becoming indistinguishable in the watery ooze lower down.

It was now necessary to decide whether these holes were made by the larvæ simply for the purpose of emerging, or whether they were more or less permanent, and used as channels of communication, or perhaps for foraging excursions, possibly at night-time. As the larvæ had nearly all emerged, I had to wait another year before I could carry on this investigation. On November 5th, 1910 (a date chosen as likely to give a prospect of finding the larvæ nearly full-fed, but not yet emerged), Mr. C. Gibbons, of Hornsby, and myself went to the swamp at Medlow. We were provided with a long-bladed draining-spade, and two large, sharp knives for cutting the sedge. The swamp was unaltered in appearance, and I soon found a large clump (marked A in the diagram) near the spot which I had examined a year previously. On cutting away the sedge level with the clump, we found three distinct, round holes. These were the entrances to three nearly vertical channels, of which two (a_1 and a_2) are shown in the diagram. By slicing away the matted roots surrounding them, we cut down to the water-level, about six inches, and then followed the channels down another foot or more, where they turned into a wider and looser horizontal channel. The latter, however, was soon lost, as it collapsed on examination. The outer channel, a_2, being in firmer mud, proceeded downwards another six inches or more, and then turned into a horizontal channel, loose, and easily destroyed like the other.

We next began to dig out the clump A at the side bordering the small depression or water-hole C. On cutting out a slab, the whole depth of the hole, we discovered a well-made channel (a_3) opening out at the side of the clump A, *below* the water-level. This was not quite vertical, and on following it down, about a foot, it turned into a softer, horizontal channel, which I took to be the same one that connected a_1 and a_2. I then followed this horizontal channel under C, where the mud was very loose and slimy. As long as there were roots enough to hold together at all, there was a distinct passage; but it collapsed almost on touching. However, it seemed to be a distinct connection, of a very flimsy kind, leading from the clump A, under C, to the clump B, and was about the right width for the easy passage of *Petalura* larvæ. Probably, in the softer ooze, the larvæ just push their way along, and leave an unstable passage-way behind them, which collapses whenever a rain-storm increases the pressure from above.

So far (after working nearly an hour) we had found no larvæ. But on dredging out the soft mud along the horizontal channel under C, we found two in quick succession, both males and fairly well-grown. I was surprised to find them so different in appearance from what I had imagined when I examined the exuviæ. They are very flabby, and appear ill-nourished. In colour, and to the touch, they are rather like the fleshy white grubs of Scarabeid beetles so commonly found when gardening. The abdomen is fleshy-white all over, except along the lateral edges of the segments and round the anal extremity, where the dark stain of the ooze seemed to have become more or less permanent. The thorax is also fleshy-white, but not quite so flabby, with a distinct orange band passing on each side from the wing-base to the mesocoxa. The head is whitish behind, but much darker on the vertex and front, and especially on the labrum, which is a hard plate, nearly black. The eyes are quite black in front. The labium is pale glaucous-greyish, with the lateral lobes and hook brownish. Wing-cases pale greyish. Femora whitish, darker on the inner side; tibiæ and tarsi fairly hard and dark. From the fact that only the front of the head and parts of the legs are hard, the rest of the insect being soft and flabby, it is clear that the insect usually inhabits the soft mud, and uses its head and legs to push itself along, and to scoop out new channels and passages in the soft ooze.

We now continued our investigation by slicing out the clump A, in a direction perpendicular to the plane of the diagram. In this way we dug out a space of six feet by three feet, including the whole of C and the adjoining side of the two clumps A and B. At the further end of C, we dug out one clump of sedge-roots containing a distinctly marked passage, from which we secured a fine larva, nearly full-fed. This was the only larva we found actually in a channel, but in most cases it was impossible to dig without stirring up the mud, and disturbing everything completely. The whole space was dug out to a depth of nearly three feet, and the mud and roots carefully dredged with the net. In all, we secured seven larvæ, ranging from about half-grown to nearly full-fed. Two of these were exceedingly weak and flabby, and died soon afterwards. On examining them, I found the whole abdomen hollow, and, in one case, the alimentary canal practically destroyed; but I was unable to find the parasite that caused this, if such were the case.

After three and a half hours' work, we finished up at the part of B opposite to A in the diagram, where we found passages opening both on the top of B (b_1, in diagram) and at its side, below the water-level (b_2). These were also explored as far as possible, and the last larva was taken about a foot below the entrance of b_2.

For examination, two larvæ were taken, and killed. The gizzards of these were cut out, and carefully examined. Firstly, *as to contents*,—the only definitely recognisable portion of the food, which had not been triturated, was, *in each case*, an Agrionid labium, which I had no difficulty in recognising as that of *Argiolestes grisea* Selys. The larvæ of this little dragonfly are very common in these swamps, but not easy to obtain with a dredging-net. They cling to the matted outcrop of fine roots at the sides of the depressions in the swamps. In the diagram, the letters Y indicate the probable spots where the larva would occur. (None were actually found in C, but they are small and inert, and we were not looking for them; I have always taken them in positions akin to Y). This seems to suggest that the *Petalura* larvæ use the channels, such as a_5 and b_2, for obtaining a supply of this Agrionid larva for food. However, if that be the case, it further suggests that they are nocturnal feeders; for they are so clumsy and slow-moving that they would have no chance of capturing the *Argiolestes* larvæ in the daytime. The latter, though by no means active, are fairly quick at dodging out of sight, behind the matted roots. It seems to me, therefore, that the *Petalura* larvæ must possess a distinct advantage over them, viz., a better power of nocturnal vision. That is probably the case. It also suggests that, during the whole of the day, they must remain in the dark, horizontal mud-channels, or low down in the vertical channels—a conclusion which is justified by the positions in which we actually found them.

What then is the value of the more numerous channels, such as a_1, a_2, and b_1, opening at the tops of the clumps? These are used for the final emergence. But, as they were found in good condition on November 5th, before any of the larvæ had emerged, they must have other uses. I think it possible that the larva may undergo each ecdysis above ground, probably during the night-time. It is also very likely that they come up these channels each night, and wander about looking for food.

The only other larvæ found, while searching for *Petalura*, were five larvæ of *Synthemis macrostigma*, two small and three nearly full-fed. These lie, just covered, in the mud of the depressions. The letters X in the diagram indicate the position. It is doubtful whether the *Petalura* larvæ ever capture them, except when they are very young. Had either of those I examined been feeding on them, the labium of *Synthemis* could not fail to have appeared in its gizzard.

Structure of the teeth in the gizzard.—The second point, and by far the most important, is the arrangement of the chitinous teeth in the Petalurine gizzard. Although nearly all the larvæ taken, appeared to be very ill-nourished and flabby, yet in both the specimens examined (I selected the two healthiest) the stomach and gizzard were very large. The latter was quite 4 mm. long, of the usual bottle-shape, the neck being about 1 mm. in diameter, and the anal end quite 3 mm. This, when carefully cleaned, cut and spread out flat on a slide, stretched out into a thin, transparent membrane in the shape of a trapezium with a base of 10 mm., top 4 mm., and slant sides 10 mm., and convexly curved. No sign of teeth could be observed, either with the naked eye or with an ordinary pocket lens. Under a magnification of 25 diameters, the teeth appeared, close up to the neck of the gizzard, and very minute. They are arranged radially in eight sets, each set containing from one to six teeth, two being by far the commonest number. The two gizzards shewed remarkable variation, as may be seen by comparing the figures (Figs.2-3). In No. 1, the arrangement was 2, 2, 2, 1, 1, 2, 2, 2. In No. 2, 4, 1, 6, 4, 2, 2, 2, 2. Clearly the number 6 is abnormal. Where more than one tooth appeared in a set, the arrangement showed a distinct beginning of longitudinal chitinisation; *e.g.*, in every case except one (the sixth set of No. 2), the second tooth of a *set of two* is placed *under* the first, not alongside it. In the two *sets of four*, found in gizzard No. 2, this tendency is also shewn, for, in one case, the four teeth are arranged longitudinally; and, in the other, the top pair only are on the same level. In the figures, the teeth are drawn disproportionately large, about four times their actual size when enlarged. Their actual measurements range from 0·02 to 0·05 mm.

This simple formation of the teeth in the gizzard of *Petalura*, is of great phylogenetic interest and importance. The gizzards of the larvæ of all the more specialised *Anisoptera* possess only four sets of teeth; each set being developed on an elongated oval layer of chitin, and the whole set being spoken of as a "fold" or "field." In *Petalura*, we have no actual chitinised fields, but only a slight development of chitin round each tooth. This formation can be easily understood from the enlarged diagrams of some of the separate sets of teeth in gizzard No. 2. From this we are able to conclude that the four fields of the more specialised *Anisoptera* have been formed by the merging, in pairs, of eight simpler fields: that the teeth were developed as chitinous protuberances, on the gizzard wall itself; and that the chitinous oval field was formed later on by the extension of the chitin at the base of each tooth, so as to include finally the whole set of teeth. In the *Petalura* gizzard we can see the beginning of the formation of a chitinous field, if we look at the enlarged figures of the teeth of the seventh and eight set (Fig.4). Here the chitin surrounds both the teeth in the set.

The tendency, shewn especially in gizzard No. 2, to form a longitudinal set of teeth, is of great interest. Amongst *Anisoptera*, the longitudinal field, containing a large number of nearly equal teeth, is a characteristic of the *Gomphinæ* only. In this respect, then, we may regard *Petalura* as shewing a connection with some distant ancestor of the *Gomphinæ*. But the difference between the two forms of gizzard is far more striking than this slight similarity, and strongly bears out the claim that the *Petalurinæ* should be regarded either as a very detached subfamily, or possibly be raised to the dignity of a family.

In a kindly criticism of my former paper on the *Petalura* exuviæ, Dr. Ris pointed out to me that there was nothing remarkable about the position of the involucre of the inferior appendage in the male *Petalura* nymph, as it is interpreted by morphologists to be part of the tergite of the eleventh abdominal segment in *Anisoptera*. Hence it should be found *above* the anal opening, and not below it; and this is actually the case. As the two involucres of the superior appendages are also morphologically portions of the eleventh tergite, there is nothing really remarkable in the inferior involucre appearing *above and between them*. He also pointed out to me that I missed a point of great interest, in not studying closely the anal end of the *Petalura* nymph; for the three caudal spines usually conspicuous in nymphs of *Anisoptera*, are here reduced to small plates, which together form a *fairly distinct and compact eleventh segment*. In Fig.6 of the Plate in my former paper (These Proceedings, 1909, Pl. xxiv.) their position is not well shewn. It would be better to examine the anal end of a *female* larva, in which the involucres of the imaginal appendages take up much less room than in the male. Such a sketch, shewing the *wide-open* anal opening, with the three plates completely enclosing it (*one* superior and *two* inferior, corresponding to the three caudal spines in other *Anisoptera* larvæ) is now given (Fig.6).

The question as to whether this larva is aquatic or air-breathing, is one of some difficulty. With several of the larvæ which I obtained at Medlow, I tried the following experiments:—

(1) They were placed in a large bottle of pure water. Those which were only about half-grown, crawled about on the bottom; but the two that were nearly full-fed, rose with the tip of their abdomens uppermost, and remained with it *just on the surface* of the water, but not pushed through into the air. I noticed particularly that the water-film covered the anal opening, and that they drew water in and out when breathing. This suggests that they preferred the best aërated water to breathe in.

(2) The larvæ were all taken out of the water, and placed in a box. Here they appeared very uncomfortable, and soon became very inert.

(3) They were next placed in a tin, in about an inch of ooze from the swamp. This seemed to suit them fairly well. They moved about somewhat quickly, breathing in large quantities of the thick mud anally, and then expelling it with such force, that I could follow the stream of particles for several inches. I noticed, in particular, that they *do not* use this strong anal expulsion as a means of locomotion, in the manner of the Aeschnid larvæ. Even when at rest, the force of expulsion was very great. This suggests that their usual method of breathing is by taking in the muddy water through the anal opening, and then, having extracted the oxygen from solution, the particles of mud are expelled with great force.

A further point of interest is, to determine what means the larva possesses of filtering the muddy water which it draws in so vigorously. If the three caudal plates that surround the anal opening be carefully opened out (as in Fig.6) it will be seen that the sides of the superior plate, and the underside of each of the inferior lateral ones, are fringed with stiff hairs. When the three plates are *in situ*, I suppose that these hairs must, in some manner, interlace to form the necessary filter, keeping the rectum itself clear of all impurities in the water. When watching the larvæ breathing in muddy water, I noticed particularly that these plates are drawn so closely together as to make the anal end appear *almost closed* during *inspiration*, yet, during *expiration*, the rectum is *wide open*, just as we find it in the exuviæ. This seems to suggest that the full-fed larva, when about to emerge, and as soon as it has climbed above the water-level, keeps its rectum open for the purpose of *air-breathing*. If this be the case, Dr. Ris' conjecture that the larva is an air-breather, is seen to have some foundation in fact, but the statement needs to be modified, *viz.*, the larvæ are only *air-breathers when above water-level*. I must confess that I fully expected the larvæ, when placed in muddy water, to push their anal ends up into the air to breathe, and I was rather surprised to find that they preferred the muddy water to anything else. Still, a little reflection will show that, even if they keep their channels of communication fairly open and clean, yet these flimsy strictures must often collapse, and during periods of heavy rain it must be quite impossible for the soft, horizontal portions to hold together. I conclude, therefore, that the larva do *usually* breathe muddy water, which is filtered as described above, and that only on special occasions, namely, when foraging above water-level, or during the final ecdysis, do they breathe air.

There is one more point of interest to determine. Do the larvæ take more than one year to reach maturity? As far as I know, practically all the imagines emerge in a period covering about the latter fortnight of November. Now, of the seven larvæ taken at Medlow, three were practically full-fed, with wing-cases of greater or less size; but the other four were considerably smaller, only, one might say, about half-grown, and shewing as yet no trace of wing-cases. It seems, therefore, probable (though not absolutely proved, for these smaller larvæ might be capable of extremely rapid development) that the imago emerges in the second year from the laying of the egg.

I have not given a drawing of the mature larva, since the drawing of the exuviæ*, in my former paper, gives a fairly good representation of it. The main difference is, that the living larva appears slightly shorter and thicker, and the wing-cases are, of course, placed much more flatly along the abdomen, the hind-wing almost completely covering both the fore-wing, and the first four abdominal segments. In conclusion, I should like to express my very sincere thanks to Mr. C. Gibbons, who so kindly accompanied me on my expedition to Medlow, and by whose help this most interesting larva was discovered.

EXPLANATION OF PLATE VII.

Fig.1.—Diagrammatic section of portion of swamp at Medlow, Blue Mountains, N. S. Wales (scale $\frac{1}{12}$), showing:—A, B, clumps of sedge; C depression or water-hole; a_1, a_2, a_3, b_1, b_2, openings of *Petalura* channels; X, X positions of larvæ of *Synthemis macrostigma*; Y, Y positions of larvæ of *Argiolestes grisea*.

Fig.2.—Teeth of gizzard of *Petalura gigantea* larva (No. 1) (much enlarged).

Fig.3.—Teeth of gizzard of *petalura gigantea* larva (No. 2) (much enlarged).

Fig.4.—*a*, *b*, *c*, Teeth of the fifth, sixth and eighth fields of No.2 gizzard, still further enlarged to show chitinisation of fields around teeth.

Fig.5.—End of abdomen of female larva of *P. gigantea*. R, rectum—I, I, involucres of imaginal appendages.

Fig.6.—Ditto, with the three caudal plates spread open, showing fringe of hairs.

* These Proceedings, 1909, pl. xxiv.